FRESHWATER SPONGES FROM A NEOTROPICAL SAND DUNE AREA

CECILIA VOLKMER-RIBEIRO, MARIA M. F. CORREIA, SERGIO L. A. BRENHA AND MAURICIO A. MENDONÇA

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A survey of a freshwater sponge community from a sand dune belt area, NE coast of Brazil, is reported for the first time. *Corvoheteromeyenia heterosclera* was the only sponge living in crystal clear seasonal ponds nestled among the sand dunes. The sponge forms fan-shaped growths around the leaves of *Eleocharis* sp.(Cyperaceae) in the shallow border of ponds, or massive crusts on sporophytic plants of *Equisetum* sp.(Equisetaceae) in deeper parts of ponds. Towards the boundary, between sand dunes and savanna (cerrado), ponds are less subject to wind action, thus more stable and allowing the establishment of shrubby vegetation and palm trees. Accumulation of decaying vegetation produces brownish acid waters in which some of the five sponge species live, all characteristic of the savanna fauna: *Metania spinata, Corvomeyenia thumi, Dosilia pydanieli, Radiospongilla amazonensis* and *Trochospongilla variabilis*. An association between two of the five savanna species with *C. heterosclera* was observed in some ponds at the verge of the mobile sand dunes. This large ecotone seems to represent the 'patch concept' in the dynamics of its ponds and their sponge communities. ❐ *Porifera, freshwater ephemeral habitats, sand dunes, savanna, ecotone, survival, dispersal, adaptations.*

Cecilia Volkmer-Ribeiro (email: ebib@pampa.tche.br), Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do sul, Cx. Postal 1188, 90.001-970, Porto Alegre - R;, and Graduate Program of Zoology, Pontifícia Universidade Católica do Rio Grande do Sul, Cx. Postal 1429, 90.619-900, Porto Alegre – R;, and Fellow Researcher of CNPq , Brazil; Maria Murlúcia Ferreira Correia, Sérgio Luis A. Brenha & Maurício Araújo Mendonça, Departamento de Biologia, Universidade Federal do Maranhão, Pr. Gonçalves Dias, 21, 65.020-240, São Luiz - MA, Brazil; *10 February 1999.*

The eastern part of Maranhão State, Brazil, is a coastal sand dune field containing an amazing array of seasonal freshwater ponds nestled among dunes, stretching along the municipalities of Tutóia, Barreirinhas and Humberto de Campos and penetrating 10-50km into the countryside where it borders with the 'cerrado' (Brazilian savanna). The National Park of 'Lençóis Maranhenses' was created in 1981 to protect the western part of this area. Under Koeppen's classification this region is classed as AW climate, with the rainy season between December-May, and the annual mean air temperature between 26.8-27.2°C.(Padua, 1983). Prior to the present work we knew nothing about the freshwater sponge fauna of this large seasonal lentic system, which appears to be unique in the world and certainly within the Neotropical Region. The study is part of ongoing investigations of the Neotropical freshwater sponge habitats and communities undertaken by the senior author and collaborators (Volkmer-Ribeiro, 1992; Volkmer-Ribeiro & Tavares,1993; Volkmer-Ribeiro et al., 1983, 1998).

MATERIALS AND METHODS

Our survey of freshwater sponges in the sand dune lentic system was undertaken at the E and W borders of the Lençóis Maranhenses, Maranhão State, Brazil (in proximity to the villages of Tutóia and Santo Amaro), with some sites inside the National Park, where sand dunes border with the savanna (Fig 1). In response to valuable information provided by local residents on current water levels (since dry and wet seasons do not occur exactly at the same period each year), our survey was conducted between 20-30 October 1995. At this time of year the largest ponds (approximately 1500m^2) contained only about 30% of their potential water capacity, which was considered an opportune time to sample because it was most likely that sponges would have gemmules.

Several variables were measured in some of the ponds in the western area (pH, temperature and salinity). The pH was taken in situ with Merck pH paper. Salinity was also recorded in situ with a salinometer. Samples of sediments were also

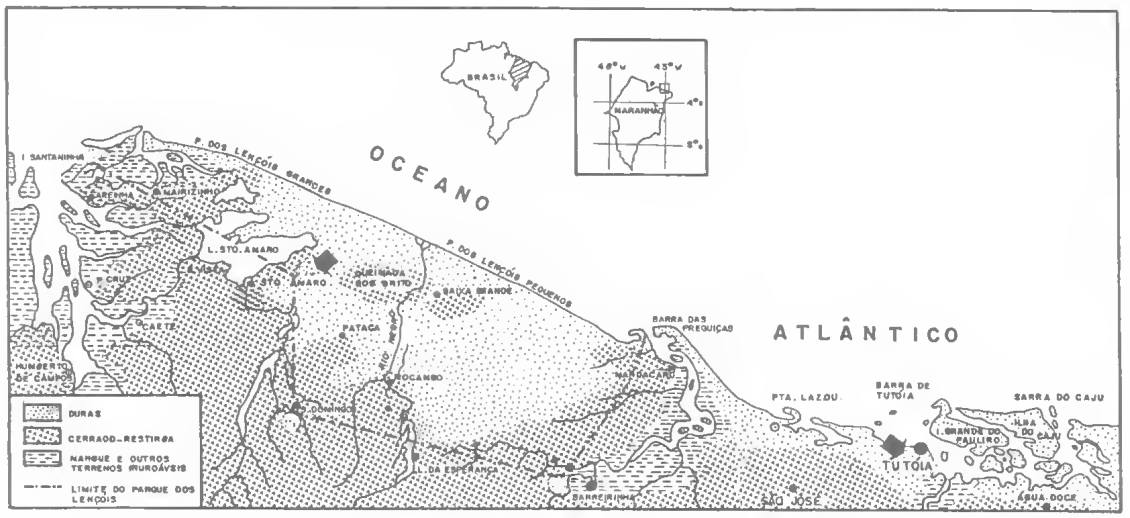

FIG. 1. The Lençóis Maranhenses. The villages of Tutóia and of Santo Amaro (arrows) are shown, at the E and W area of the Lençóis Maranhenses, respectively, as well as the National Park limits and the contact areas with the savanna.

collected from the top layer of pond beds, stored in small glass jars, for ponds in which sponges were not conspicuous. This was undertaken in order to determine, through the presence of spicule sediments, whether sponges had ever been present in these ponds (Volkmer-Ribeiro & Turcq, 1996). These sediment samples are also currently being used by the senior author to study recent and paleo sediments. Entire or cross-sectioned dry specimens of *C. heterosclera* were glued to a stub and gold-coated for scanning electron microscope (SEM) observations and photographed on a MCN JEOL-5200 microscope equipped with a Pentax SF7 35mm camera. Part of the dry specimens was deposited in the collection of Departamento de Biologia of Universidade Federal do Maranhão. The other part was deposited in the Porifera Collection of Museu de Ciências Naturais of Fundação Zoobotânica do Rio Grande do Sul (MCN/POR) with Catalog numbers listed in Tables 1 and 2.

RESULTS

A succession of ponds with different spatial areas (Fig. 2A-C) and water color was observed as one progressed from the mobile dunes towards the savanna boundary. Ponds situated among the

TABLE 1. Identification of the sponges sampled at the ponds from the E area of Lençóis Maranhenses, together with their environmental characteristics and substrates.

Ponds sampled around Tutóia Village	Type of sample	Environment	Substrate	Water color	Sponge species	Catalog number MCN/POR
Lagoa do Vidro	specimens	sand dunes	*Equisetum* sp	clear	*Corvoheteromeyenia heterosclera*	3829-3840
Lagoa da Ponta do Arpoador	specimens	sand dunes	*Eleocharis* sp	clear	*Corvoheteromeyenia heterosclera*	3830-3839
Lagoa da Pedra Hume	sediment	sand dunes		brownish clear	*Radiospongilla amazonensis, Trochospongilla variabilis, Corvoheteromeyenia heterosclera*	3854-3856
Lagoa da Ponta do Mangue	bottom sediment	oasis		brownish	*Radiospongilla amazonensis, Trochospongilla variabilis*	3859
Lagoa da Coceira	sediment	grassy field		black	*Corvomeyenia thumi, Metania spinata*	3858

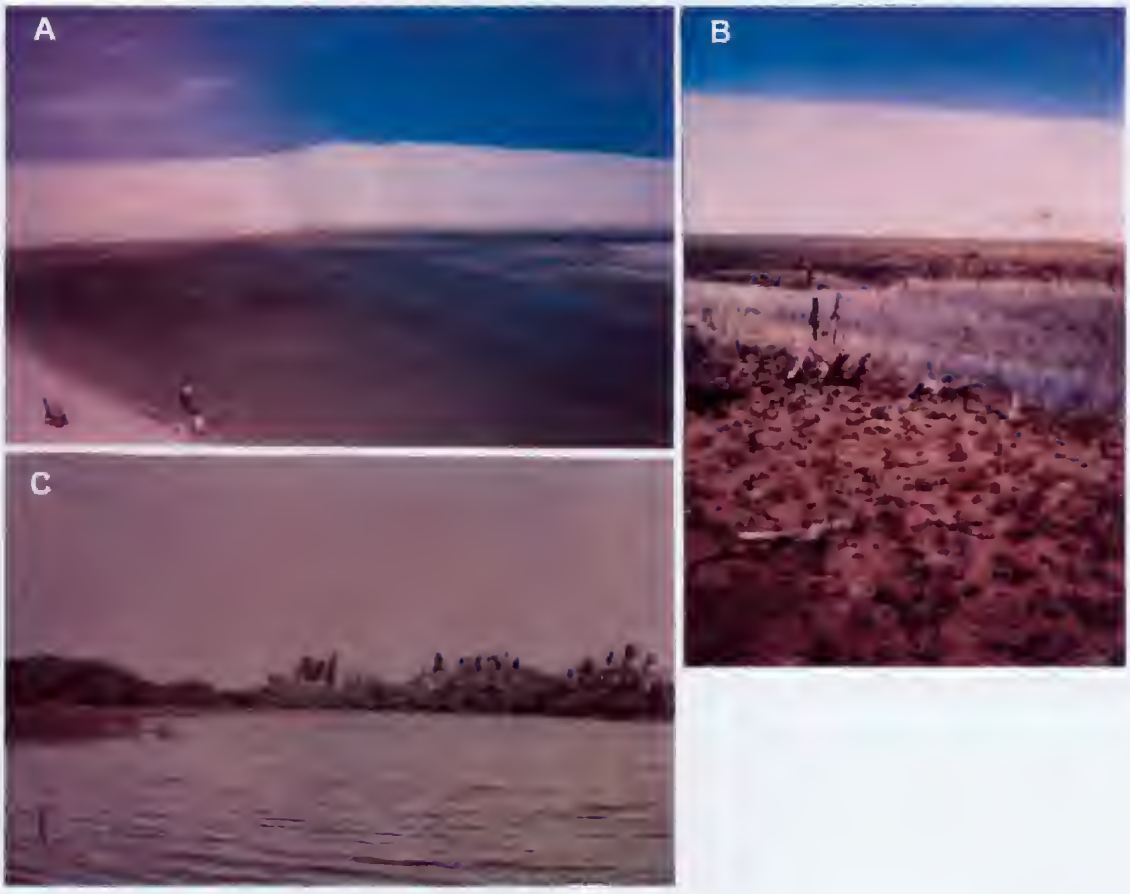

FIG. 2. Study area. A, Lagoa do Vidro, at the E boundary of the Lençóis Maranhenses. B, Lagoa da Ponta do Arpoador, showing the stiff Cyperacean vegetation exposed to the sun as the pond becomes fully dry. C, Lagoa do Pico, at the western border of the Lençóis, with its surrounding dunes covered by bushy vegetation and palm trees (photos C. Volkmer Ribeiro).

mobile dunes had crystal clear waters whereas those approaching the savanna boundary had increasingly brownish color and acidic pH (Tables 1-2).

Lagoa do Vidro (Fig. 2A), Lagoa da Ponta do Arpoador (Fig. 2B) and Lagoa do Cajueiro are clear water ponds amongst the mobile dunes. The dominant plants in these ponds, as potential sponge substrates, were *Eleocharis* sp. and *Equisetum* sp. The former plant is a small but very abundant Cyperaceae which inhabits the shallow marginal area of ponds, and is the first to emerge from the water (Fig. 2B) as ponds begin to dry up. The second species is also relatively abundant in deeper parts of ponds, close to the leeward face of the barchan dunes (Fig. 2A).

Lagoa da Pedra Hume, Lagoa da Ponta do Mangue, Laguinho, Lagoa do Pico (Fig. 2C) and Lagoa da Coceira represent a succession of ponds having brownish clear to black water, and distributed from the mobile sand dunes into the almost flat, fixed dunes, covered with grassy or bushy vegetation. Lagoa da Ponta do Mangue is an oasis pond with surrounding patches or islands of palm trees and containing shrubby vegetation. Lagoa da Coceira was reduced to a fetid, tiny muddy pond with black water surrounded by grass. Laguinho was a relatively deep pond, and together with Lagoa da Ponta do Mangue, is a popular fishing site.

Taxonomic identification of the sponges sampled in the E and W dune areas are presented in Tables 1 and 2, respectively, together with their

TABLE 2. Identification of the sponges sampled at the ponds from the W area of Lençóis Maranhenses, together with their environmental characteristics and substrates.

Ponds sampled around Santo Amaro Village	Type of sample	Environment	Substrate	Water color	Sponge species	Catalog number MCN/POR
Lagoa do Cajueiro (pH 6; salinity 1%, water temperature 28.5°C at 10am)	Specimens & sediments	sand dunes	*Eleocharis* sp	clear	*Corvoheteromeyenia heterosclera*	3853
Laguinho	Specimens	sand dunes	stones	brownish clear	*Dosilia pydanieli*	3857
Lagoa do Pico (pH 5.5; salinity 0.5%, water temperature 32°C at 0.10pm)	Specimens & sediments	sand dunes with bushy vegetation	submersed branches of riparian bushes (*Crysobalanus icaco*)	brownish	*Metania spinata*, *Corvomeyenia thumi*, *Trochospongilla variabilis*, *Radiospongilla amazonensis*	3089

environmental characteristics and substrates. Ponds in which only sediments were reported indicate that living samples of sponges were not found. These tables indicate that *Corvoheteromeyenia heterosclera* and *M. spinata* were abundant, as were gemmules, particularly in the two extremes of the 'pond succession' (i.e. very clear ones and the brownish colored ones), confirming that the sampling period was well chosen and our prediction that this huge seasonal lentic system contained such a fauna.

The pond sponge communities also revealed interesting distribution patterns. The only species found in clear-water sand dune ponds was *C. heterosclera* (Ezcurra de Drago, 1974), with fan-shaped growths on the leaves of the Cyperaceae *Eleocharis* sp. (Fig. 3A) at the pond margins (Fig. 2B), or thick irregular growths on the sporophitic plants of *Equisetum* sp.(Fig. 3B) in deeper parts of the pond close to the leeward dune face (Fig. 2A). Sponges on both substrates were fully developed and full of gemmules. Many specimens were seen dried out, not far from the pond margin, their gemmules continually swept away by the wind. On the other hand specimens still submerged at the pond margins were already half buried by sand blown in from the dune, the same way as were specimens encrusting *Equisetum* located close to the dune inner wall. *Corvoheteromeyenia heterosclera* appears to be a species fully adapted to such an environment. SEM study of cross sections of *Eleocharis* leaves encrusted with this species (Fig. 3C) disclosed a skeletal structure of very slim fibers producing a very open and irregular network enclosing sand grains of variable sizes. The presence of oscular sieves (Fig. 3D) is another device used to prevent oscula being clogged with sand. Gemmoscleres were also seen to take part in skeletal fibers, together with megascleres and two categories of microscleres (Fig. 3E-F), which might be due to the accelerated production of gemmules during this time of the year. Living specimens of *C.heterosclera* had a light green color, probably due to its association with a microscopic green algae, and this green color could be seen around the pond margins where sponges had been buried and were decaying in the sand.

The sponge community towards the savanna boundary included one or more of the following species, but never all five of them: *Metania spinata* (Carter, 1881), *Corvomeyenia thumi* (Traxler, 1895), *Dosilia pydanielli* Volkmer-Ribeiro, 1992, *Trochospongilla variabilis* Bonetto & Ezcurra de Drago, 1973, and *Radiospongilla amazonensis* Volkmer-Ribeiro & Maciel, 1983. However, leaving this area and heading towards the clear-water ponds we observed associations of *C. heterosclera* with *R. amazonensis* and *T. variabilis*.

TAXONOMIC REMARKS. Ezcurra de Drago (1979) erected *Corvoheteromeyenia* for *Corvomeyenia australis* Bonetto & Ezcurra, 1966, and *C. heterosclera* Ezcurra de Drago, 1974. The holotype of the first species comes from Laguna Setúbal, next to the town of Santa Fé, Argentina, whereas the holotype of the second species comes from NE Brazil, with no precise locality data. The distinction between the two species was based particularly on their respective gemmoscleres, which are composed of two categories differing in size and shape in the first species, and one category in the second species. Specimens from the Lençóis Maranhenses agree with the second species in spiculation and geographical origin. *Corvoheteromeyenia heterosclera* has also been collected from other sand dune or paleo sand dune areas in S Brazil (Volkmer-Ribeiro, unpublished data), and its spicular remains may be useful indicators of such environments.

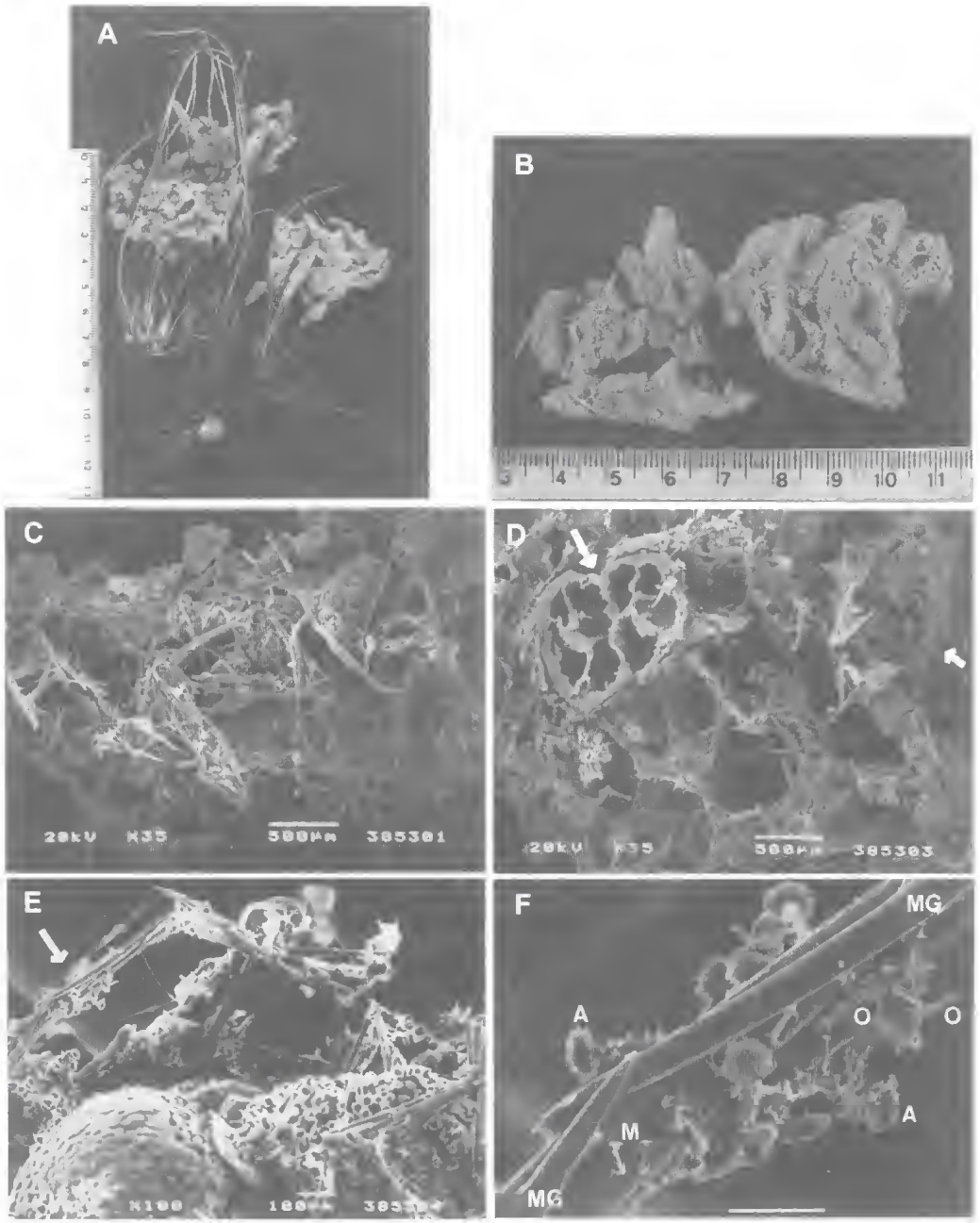

FIG. 3. Freshwater sponges. A, Fan-shaped specimens of *Corvoheteromeyenia heterosclera* full of gemmules growing on *Eleocharis* sp. B, Specimens of *Corvoheteromeyenia heterosclera* growing on *Equisetum* sp. C, Skeleton of *Corvoheteromeyenia heterosclera* with an open network where sand grains are enclosed side-by-side with the gemmules. D, Cross section of a leaf of *Eleocharis* sp. (arrow, upper left) encrusted by the skeleton of *Corvoheteromeyenia heterosclera*, showing an irregular distribution of the thin skeletal fibers and (arrow, upper right) the presence of an oscular sieve. E, Skeleton of *Corvoheteromeyenia heterosclera* with two gemmules in the process of completion at the bottom as well as abundant free gemmoscleres (arrow). F, Skeletal fiber of *Corvoheteromeyenia heterosclera* (see arrow in Fig. 3E) showing the reduced amount of spongin and the presence of the two categories of microscleres (O, microspined oxea; M, microanfidiscs) and several large anfidisc gemmoscleres (A) around the megascleres (MG).

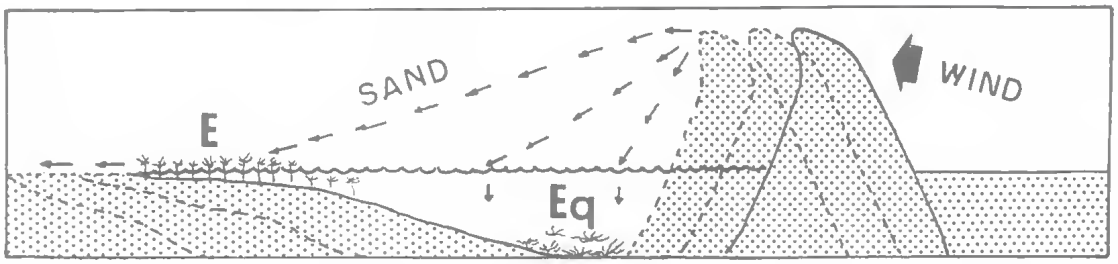

FIG. 4. Schematic drawing of the wind-driven dynamics that seasonal ponds around the moving dunes of Lençóis Maranhenses are subjected to, together with the vegetation and sponges they contain. E= *Eleocharis*, Eq= *Equisetum*.

DISCUSSION

Recent literature dealing with the study of Neotropical freshwater sponge communities has shown that the five species recorded in the present study, found in the ponds close to the savanna boundary, generally thrive in seasonal ponds N to S throughout the Brazilian savanna (Volkmer-Ribeiro, 1992; Volkmer-Ribeiro et al., 1998). Thus, two characteristic faunal assemblages are present: one in the savanna ponds with five species, and one which is monospecific and lives in the sand dune ponds.

Observations made here on the characteristics of *C. heterosclera* match well with our present understanding of the processes associated with constant disturbances imposed by dune movement on populations. The living barchan dunes, which move in the direction of the wind in coastal areas, is a well known geomorphological phenomenon (Termier & Termier, 1963). The Lençóis Maranhenses is, however, unique in its situation being in a tropical area with a marked rainy season, resulting in temporary accumulation of water in ponds on the leeward sides of moving dunes, with the ponds subsequently displaced next season. The wind, which was seen to blow the sand into the ponds, was also seen to blow ahead the gemmules from dry, exposed sponges growing on *Eleocharis* at the perimeter of ponds. Moreover, the erect position of plant leaves together with the fan-shaped morphology of the sponges appears to facilitate gemmule dispersal via wind action. These are the pioneers of new sponge populations, opportunistically waiting in place where the new border of the pond with *Eleocharis* will be situated next season. The same process applies to sponges encrusting on *Equisetum*, which will be passed over by the moving dune when again they will be set against the inner side of a barchan dune, protected against drought and ready to again form the *Equisetum/Corvoheteromeyenia* association (Fig. 4).

The region extending between the areas occupied by these two faunas thus biologically and physically defines a savanna/sand dune ecotone. This particular ecotone best fits the dynamic 'patch concept' (White & Picket, 1985), driven by constant disturbance through dune movement. The Lençóis Maranhenses is an outstanding example of the patch concept with its pond system, spatial and temporal relationships to dune movement, and dynamic sponge fauna. It also illustrates the remarkable ability of freshwater sponges to manage constant disturbance via asexual reproduction when gemmules produced by these sponges are especially selected mechanisms to withstand drought and to passively disperse via the wind, enabling all six species to opportunistically colonise new pond systems as they develop.

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